SEED DISPERSAL BY BIRDS AND DENSITIES OF SHRUBS UNDER TREES IN ARID SOUTH AUSTRALIA

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Summary

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The frequencies of nine species of shrub under *Acacia papyrocarpa* trees, under *Myoporum platycarpum* trees and in the spaces between trees were measured in a South Australian arid zone woodland. All nine species were at least as common under the trees as they were in the open, and five species had significantly higher frequencies under the trees. Three species with higher frequencies under trees, *Chenopodium gaudichaudianum*, *Enchylaena tomentosa* and *Rhagodia spinescens*, produce fleshy fruits that are consumed by birds. Their seeds would tend to be disseminated under trees in which the birds perch. *Enchylaena tomentosa* was equally abundant under both three species, but *R. spinescens* and *C. gaudichaudianum* were more abundant under *A. papyrocarpa* than under *M. platycarpum*. Traps set under the canopies of the two tree species collected similar though highly variable numbers of seeds. This suggests that rates of seed germination or seedling survival for *R. spinescens* and *C. gaudichaudianum* are higher under *A. papyrocarpa* than *M. platycarpum*. The distribution of these two shrubs cannot be explained solely by the pattern of seed dispersal by birds. For *Enchylaena tomentosa*, seed dispersal by birds may provide an adequate explanation for its distribution.

KEY WORDS: Chenopodiaceae, seed dispersal, plant distribution, birds, fleshy fruits.

Introduction

In the Australian arid zone, a variety of shrubs ("berry chenopods") and small trees (*Acacia*, *Exocarpus*, *Heterodendrum*) produce brightly-coloured fleshy fruits or arils that are consumed by birds (Davidson & Morton 1984; Forde 1986). Many of the shrubs (e.g. *Rhagodia spinescens*, *Enchylaena tomentosa* and *Chenopodium gaudichaudianum*) are found at higher frequencies underneath trees and large shrubs than in the open (e.g. Barker 1972[3]). Two hypotheses have been proposed to account for this. First, the clumped distribution reflects the pattern of dissemination by birds, the birds defaecating seeds while perched in trees (e.g. Osborn *et al.* 1935; Leigh & Mulham 1965; Forde 1986). Alternatively, or in addition, Barker (1972)[3] suggested that the clumping was due to more favourable growing conditions beneath tree canopies. To distinguish between these two hypotheses requires measuring the seed rain beneath and between tree canopies, and determining rates of germination and seedling establishment in the different microenvironments.

In this paper, we (1) document the distribution of several species of shrubs in relation to tree canopies on Middleback Station, 21 km north-west of Whyalla; and (2) report the use of a "seed trap" to measure the seed rain beneath trees due to birds and discuss the data so derived.

Materials and Methods

Study site

The study site was in the south-western corner of Overland Paddock, Middleback Station (32°57'S, 137°24'E) in an area of open woodland which is moderately grazed by sheep. Two tree species predominated: *Myoporum platycarpum* R.Br. which grows to 10 m and has a thin elevated canopy; and *Acacia papyrocarpa* Benth. which has a dense low spreading canopy. The two trees were infected by mistletoes: *M. platycarpum* by *Lysiana exocarpi* (Behr) Tiegh. and *A. papyrocarpa* by *Amyema quandang* (Lindl). Teigh. The understorey was dominated by the chenopods, *Maireana sedifolia* (F.Muell.) P. G. Wilson, *Atriplex vesicaria* Heward ex Benth., *Maireana pyramidata* (Benth.) P. G. Wilson and *Rhagodia ulicina* (Gand.) P. G. Wilson. Four species of small shrubs (*Rhagodia spinescens* var. *spinescens* F.Muell., *Chenopodium gaudichaudianum* (Moq.) P. G. Wilson, *Enchylaena tomentosa* R.Br., *Lycium australe* F.Muell.), the two

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[3] Barker, S. (1972) "Effects of Sheep Stocking on the Population Structure of Arid Shrublands in South Australia". Ph.D. thesis. University of Adelaide, Adelaide. Unpubl.

mistletoes and two small trees or large shrubs, *Exocarpus aphyllus* R.Br. and *Heterodendrum oleaefolium* Desf., produced fruits that were consumed by birds in the area (Reid 1984[4]; Forde 1986).

Distribution of shrubs

Distribution of shrubs in three zones: under the canopies of *M. platycarpum*, under the canopies of *A. papyrocarpa*, and in the spaces between the trees and large shrubs was measured. Interspaces were at least 2 m from the canopy of any tree or large shrub. Two hundred 0.5 m × 0.5 m quadrats were placed haphazardly in each zone, and the presence of a shrub species in each quadrat was scored if any part of its canopy occurred in the quadrat. The diameters of the canopies of 30 individuals of each shrub species in each zone was measured by measuring the width across the plant along two axes (north-south and east-west). Since the mean canopy diameter of a particular shrub species was the same under the two tree species as well as in interspaces, incidence in quadrats provides a measure of the relative density of a plant species in each of the three zones. However, the canopies of the different shrub species were not the same diameter (Table 1), so the relative densities of the different species cannot be determined from the quadrat frequencies.

[4] Reid, N. (1984) "The Role of Birds in the Reproduction of an Arid Zone Population of Grey Mistletoe *Amyema quandang* (Loranthaceae)." Ph.D. thesis. University of Adelaide, Adelaide. Unpubl.

Trapping for bird droppings

Twenty-two traps to collect bird droppings were deployed in March 1984. Traps were made by tying 1.2×1.5 m sheets of terylene voile (mesh 0.8× 0.3 mm) to steel stakes to form a catching area of 1.0×1.5 m that stood 90 cm above the ground (e.g. see Sorensen 1981). This was the largest size of trap that could be conveniently erected under the canopies of the trees. A stone was placed in the centre of the catching area to prevent spillage of seeds by strong winds. Equal numbers of traps were placed beneath canopies of mature *M. platycarpum* and mature *A. papyrocarpa*. All of these trees were infected with variable amounts of mistletoes. Traps were inspected and emptied of seeds at two 4-monthly intervals. The seeds were identified using a reference collection of seeds compiled in the area. Many of the traps were damaged 4 to 8 months after deployment and observations ceased after 8 months.

Results

Distribution of shrub species in Overland Paddock

Nine species of shrubs were detected in the six hundred 0.5×0.5 m quadrats. Of these, five species occurred significantly more frequently under the canopies of either *Acacia papyrocarpa* or *Myoporum platycarpum* than in the interspaces between the trees and large shrubs (Table 1). Of these, three species produced fleshy fruits that were dispersed by birds (*Chenopodium gaudichaudianum*, *Enchylaena tomentosa* and *Rhagodia spinescens*), while the other two species (*C. desertorum* and

TABLE 1. *Frequency of occurrence of shrubs in 200 quadrats (0.5×0.5 m) in each of three zones in Overland Paddock, March 1984.*

Shrub species	Mean canopy[a] area (m^2)	Frequency in 200 quadrats: beneath *A. papyrocarpa*	beneath *M. platycarpum*	in interspace	X^2 value[b]
Atriplex vesicaria	0.40	38	74	44	14.3 ***
Chenopodium desertorum	—	12	10	2	6.0 *
C. gaudichaudianum[c]	0.17	51	16	0	60.9 ***
Enchylaena tomentosa[c]	0.11	32	34	7	18.6 ***
Lycium australe[c]	0.49	7	8	13	2.2 NS
Maireana pyramidata	—	11	11	11	0.0 NS
M. sedifolia		42	42	34	1.1 NS
Rhagodia spinescens[c]	—	41	22	0	40.1 ***
R. ulicina	—	23	32	18	4.1 NS

[a] Canopy areas calculated from diameters of 60 or 90 individuals depending on number of zones in which plant species occurred. Standard errors were less than 30% of the mean and there were no significant differences in the canopy area of a shrub species in different zones (ANOVAs, $P \geq 0.05$), so data for the different zones were pooled.
[b] The X^2 statistic (2 *d.f.*) tests the null hypothesis that shrub species were evenly distributed across the three zones:
* $P \leq 0.05$
** $P < 0.01$
*** $P < 0.001$
NS not significant
[c] Shrubs that produce fleshy fruits consumed by birds.

Atriplex vesicaria) had wind or ant-dispersed seeds. *Enchylaena tomentosa* and *C. desertorum* were equally frequent under both canopies, but *A. vesicaria* was encountered most frequently under *M. platycarpum*, and *C. gaudichaudianum* and *R. spinescens* were encountered most frequently under *Acacia papyrocarpa*.

Four species of shrub showed no significant clumping under the canopies of trees (χ^2 tests, $p>0.05$). Of these, the *Maireana* species and *R. ulicina* have wind or ant-dispersed seeds but *Lycium australe* produces fleshy fruits that are dispersed by birds and perhaps reptiles.

Seed rain detected by traps

Table 2 lists the quantity of seeds collected in the traps set under the canopies of *Acacia papyrocarpa* and *M. platycarpum* during two time periods. The numbers of seeds deposited per trap was highly variable, with variances often exceeding the means. There was no significant difference in the total numbers of seeds deposited under *A. papyrocarpa* and *M. platycarpum* (rank-sum tests, $p>0.05$). More seeds were caught during the period July–November than between March–July (rank-sum test, $p<0.002$). In general, the number and species of seeds being deposited during each period reflected the fruiting seasons of the plants. *Chenopodium gaudichaudianum*, *Enchylaena tomentosa* and *Exocarpus aphyllus* fruited mainly during winter and early spring, while *Heterodendrum oleaefolium* and *Lycium australe* fruited mainly in autumn. *Rhagodia spinescens* fruited mainly during summer, but like *Enchylaena tomentosa* and *Exocarpus aphyllus*, produced small quantities of fruit throughout most of the year.

Many of the traps also collected seeds of mistletoes. These data are not presented since mistletoe seeds must be deposited on the branches of host trees to be effectively disseminated. The seeds collected in the traps therefore represented ineffective dispersal.

Discussion

The purpose of this study was to measure the distribution of shrubs, particularly the fleshy-fruited chenopods, in relation to tree cover, and to determine the usefulness of traps in measuring seed rains. Prior to this study, statements that fleshy-fruited shrubs were clumped under trees were based largely on qualitative observations (e.g. Osborn *et al.* 1935; Leigh & Mulham 1965; Forde 1986). Our quadrat data show that three fleshy-fruited shrubs were found mainly under trees, and that the extent of this clumping varied from species to species. *Rhagodia spinescens* and *Chenopodium gaudichaudianum* were almost exclusively found under tree canopies, but more frequently under *Acacia papyrocarpa* than under *Myoporum platycarpum*. *Enchylaena tomentosa* was found with equal frequency under both tree species and occasionally in interspaces, while *Lycium australe* was equally abundant under trees and in interspaces (Table 1). However, clumping beneath trees was not restricted to bird-dispersed species. Among the shrubs dispersed by wind or ants, *Atriplex vesicaria* was more common beneath *M. platycarpum* than *Acacia papyrocarpa* or in interspaces, and *C. desertorum* was significantly more common under both trees than in the interspaces. Higher densities of shrubs under trees could occur because (1) more seeds are dispersed beneath trees and/or (2) germination rates and seedling establishment are

TABLE 2. *Numbers of seeds deposited by birds in traps set under* Myoporum platycarpum *and under* Acacia papyrocarpa *in Overland Paddock under two time periods in 1984.*

Species of shrub	Mean number of seeds per trap ± S.E. March–July	July–November
Traps set under *M. platycarpum*	n = 11	n = 4
Chenopodium gaudichaudianum	0.3 ± 0.2	4.8 ± 3.3
Enchylaena tomentosa	2.3 ± 2.0	10.5 ± 3.5
Exocarpos aphyllus	5.7 ± 3.1	23.5 ± 10.9
Heterodendrum oleaefolium	3.2 ± 1.4	0.0 ± 0.0
Lycium australe	0.4 ± 0.2	0.0 ± 0.0
Rhagodia spinescens	1.1 ± 0.7	0.2 ± 0.3
Total	12.9 ± 7.2	39.0 ± 7.1
Traps set under *A. papyrocarpa*	n = 11	n = 8
Chenopodium gaudichaudianum	0.0 ± 0.0	0.4 ± 0.4
Enchylaena tomentosa	1.4 ± 0.7	5.8 ± 3.7
Exocarpus aphyllus	5.8 ± 3.8	28.4 ± 9.2
Heterodendrum oleaefolium	1.7 ± 0.8	0.6 ± 0.5
Lycium australe	0.2 ± 0.2	0.0 ± 0.0
Rhagodia spinescens	0.4 ± 0.4	1.1 ± 1.1
Total	9.5 ± 4.6	36.2 ± 14.2

higher under trees than in the open (e.g. Barker 1972[3]; Forde 1986). These two explanations are sequential and not mutually exclusive. Both are probably important in determining the distributions of various fleshy-fruited plants in Overland Paddock. The first thing to demonstrate, however, is whether birds disperse seeds mainly to sites under trees.

On Middleback Station, fleshy-fruited shrubs have their seeds dispersed largely by birds and most of the seeds appear to land under trees. Although our traps were not deployed to demonstrate that more seeds were deposited under trees than in the open, other observations enable such a conclusion. In Overland Paddock, two species of honeyeater are largely responsible for the dispersal of seeds by birds, the Spiny-cheeked (*Acanthagenys rufogularis*) and Singing (*Lichenostomus virescens*) Honeyeaters (Reid unpubl.). These honeyeaters mainly feed on the nectar and fruit of mistletoes, supplementing these foods with insects and fruits of other shrubs (Reid 1984[4]). More than 90% of their faeces are discharged while the birds are perched more than a metre above the ground in trees or tall shrubs (Reid unpubl.). Consequently bird-disseminated seeds should be concentrated under the canopies of trees.

The traps that we deployed under the trees were successful in collecting seeds, and the quantities collected (10–30 seeds/m^2/4 months; Table 2) are consistent with estimates of the numbers of seeds that should have been voided by birds. Assuming that there were 1.2 honeyeaters/ha, that these honeyeaters consumed 80–160 seeds from fleshy-fruited shrubs per day, that the birds largely disseminated these seeds under the canopies of trees and that the tree cover was 10%, then in 4 months approximately 10–20 seeds/m^2 should have been voided by birds under trees (Reid 1984[4], in prep.).

The numbers of seeds collected by individual traps were highly variable. Two potential sources of variation probably account for this; variation in the use of trees or parts of trees by birds, and variation in faecal composition. Certain trees or parts of trees may be used more extensively by birds because of their location, architecture or the amount of food associated with them. Trees centrally-located in a bird's territory or near the bird's nest may be used more frequently (e.g. Orians & Pearson 1979). The density of the foliage or height of a tree may provide birds with better protection from exposure or predators, or better vantage points for detecting predators or intruders, and so trees with these attributes may be used more frequently. The trees in the study area also differed in the numbers of mistletoes they supported (Reid 1984[4]) and probably also in the quantities of fleshy fruits provided by the shrubs beneath them. Birds should spend more time in trees where the food supply is greatest (e.g. Charnov 1976; Pyke *et al.* 1977). The second major source of variation concerns the faeces of the birds. A single faecal dropping may contain 0 to 20 seeds, and much of the variation between traps may be due to variations in the numbers of seeds in a faecal dropping rather than variations in the use of trees by birds. We counted the total number of seeds in the traps, not the number of faeces. Future studies may wish to control for these variations, or at least account for them by recording the architectural features, the locations, and associated food supplies of the trees under which the traps were placed. Use of several traps under the same tree also would allow within-tree variation in bird use to be measured.

The size and design of the traps seems appropriate for measuring seed rains under trees in the arid zone. Traps, however, would need to be set closer to the ground and under shrubs if seed rains were to be measured in the interspaces between trees, because the honeyeaters only defaecate while perched (Reid 1984[4]). The size of the traps (1.5 × 1.0 m) also seems appropriate since larger traps would have been too awkward to erect under trees and the size was such that there was a reasonable chance that a trap would collect at least some seeds. Traps failed to collect seeds on only six occasions out of 34 four-month exposures. Based on our experience, we would recommend clearing traps of their seeds every two months, and using a stronger mesh for the catching material. This would reduce the loss of faecal material due to the catching material deteriorating with time. We found that terylene voile deteriorated after about four months, particularly under *Myoporum platycarpum* where the traps were exposed to more sunlight.

Given that most of the seeds are dispersed to sites under trees we would expect bird-dispersed plants to be most abundant under trees in the arid zone. In general this is the case, but there are exceptions. *Lycium australe* was equally abundant under trees and in interspaces, and the low clonal tree, *Heterodendrum oleaefolium*, often occurs away from other trees. These species reproduce extensively by root suckers and are apparently long-lived relative to the trees (Purdie 1969[5]; D. E. Symon pers. comm.). Little is known about their seedling recruitment (cf. suckering), since seedlings are rarely seen: no seedlings of *H. oleaefolium* have

[5] Purdie, R. (1969) "The Population Structure of Selected Arid Zone Tree Species". B.Sc.(Hons) thesis, Univ. of Adelaide. Unpubl.

been detected on Middleback Station over the last 20 years (Lange unpubl.). Seedlings of these species may only establish under trees, but once established, may produce suckers to exploit interspaces between trees where competitive interactions with the established trees presumably are reduced. The present distribution of these plants, then, may not reflect the sites where seedlings established, and the relatively high densities of these plants away from trees is not necessarily inconsistent with most of the seeds being deposited under trees. In addition, *Lycium australe* produces fruit close to the ground and lizards may therefore consume and disperse some *Lycium* seeds to interspaces.

The best evidence that factors other than seed dissemination by birds are also involved in the eventual pattern of distribution in these fleshy-fruited plants comes from comparing the distributions of the three berry chenopods, *Rhagodia spinescens*, *Chenopodium gaudichaudianum* and *Enchylaena tomentosa*. These three species are almost exclusively bird-dispersed, and similar quantities of seeds were deposited under *A. papyrocarpa* and *M. platycarpum* (Table 2). The density of *Enchylaena tomentosa* under the two tree species was similar, and so the pattern of seed dispersal by birds may provide an adequate explanation for its distribution. However, both *R. spinescens* and *C. gaudichaudianum* had higher densities under *A. papyrocarpa* than *M. platycarpum*. Factors besides dispersal by birds are needed to explain this. The most likely explanations involve the climatic or edaphic differences encountered beneath trees, coupled with differences in the regeneration niche of the shrubs. *Acacia papyrocarpa* and *M. platycarpum* differ in architecture (branching pattern etc.) and hence in the amount of shade they provide a germinating seed or seedling. The canopy of *A. papyrocarpa* is relatively dense and provides shade and a thick cover of litter. *Myoporum platycarpum* has a high thin canopy, so plants beneath it are subject to conditions of more severe water stress (Barker 1972[3]). Other factors such as increased nutrient cycling under *A. papyrocarpa* (Correll 1967[6]) or increased grazing pressure under *M. platycarpum* could also be involved. Similar sorts of factors would account for the fact that *Atriplex vesicaria* and possibly *Rhagodia ulicina* were more abundant under *M. platycarpum* than *A. papyrocarpa*. Careful field experiments will be required to determine the factors (edaphic, climatic, biotic) that are important for the germination and seedling establishment of each species. These experiments should involve transplanting seeds or seedlings between the canopies of different tree species as well as into the interspaces. Only after these experiments have been performed will we have the necessary evidence to state the relative contributions of bird dissemination of seeds and environmental factors in determining the distribution of fleshy-fruited shrubs in the arid zone.

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A PROPOSED REFERENCE SECTION FOR THE TORTACHILLA LIMESTONE

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Summary

Roadside outcrops of sedimentary rocks near Port Noarlunga, South Australia, are identified as Late Eocene stratigraphic units of the Noarlunga Embayment within St Vincent Basin. Fossil planktonic and benthic foraminifera from these rocks compare favourably with stratotype Tortachilla Limestone and the Tuketja Member of Blanche Point Formation. An exposure of highly fossiliferous, glauconitic calcarenite, bounded below by the South Maslin Sand Member of Maslin Sands, and above by the Tuketja Member of Blanche Point Formation, is proposed as a reference section for Tortachilla Limestone.

KEY WORDS: Eocene, foraminifera, Noarlunga Embayment, St Vincent Basin, Tortachilla Limestone.